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Old-growth forest versus generalist lichens: Sensitivity to prolonged desiccation stress and photosynthesis reactivation rate upon rehydration

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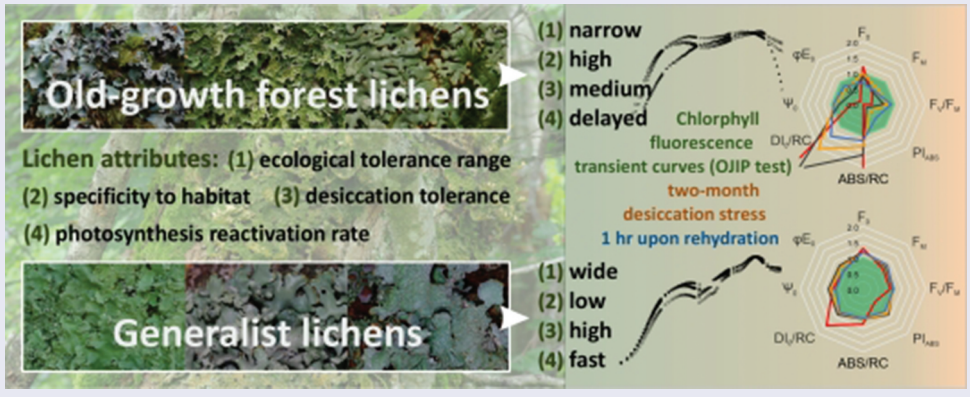
ABSTRACT

Most epiphytic lichens demonstrate high specificity to a habitat type, and sensitive hygrophilous species usually find shelter only in close-to-natural forest complexes. Some of them are considered as old-growth forest and/or long ecological continuity indicators. To evaluate general links between the narrow ecological range and physiological traits, two distinct sets of model lichens, i.e., old-growth forest (*Cetrelia cetrarioides* (Duby) W.L. Culb. & C.F. Culb., *Lobaria pulmonaria* (L.) Hoffm., *Menegazzia terebrata* (Hoffm.) A. Massal.), and generalist (*Flavoparmelia caperata* (L.) Hale, *Hypogymnia physodes* (L.) Nyl., *Parmelia sulcata* Taylor) ones, were examined in terms of sensitivity to long-term desiccation stress (1-, 2-, and 3-month) and photosynthesis activation rate upon rehydration. Desiccation tolerance and response rate to rehydration are specific to a given ecological set of lichens rather than to a particular species. Noticeable delayed and prompt recovery of high photosynthetic activity of photosystem II (PSII) characterize these sets, respectively. At the same time, although a decrease in the potential quantum yield of PSII in lichen thalli with a relative water content (RWC) at the level of 25% was observed, the efficiency remained at a very high level for all species, regardless of habitat preferences. Among the examined lichens, the fluorescence emission parameters for *F. caperata* were the fastest toward equilibrium upon rehydration, both after a shorter and a longer period of desiccation stress. In contrast to generalist lichens, retrieving of photosynthesis after 3-month desiccation failed in old-growth forest lichens. In the long term, prolonged rainless periods and unfavorable water balance in the environment predicted in the future may have a severely limiting effect on hygrophilous lichens during growing season (also in the sense of species associations) and, at the same time, promote the development of generalists.



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INTRODUCTION

The advantage deriving from living in the stable symbiotic association allowed lichens to spread throughout the world and grow in a variety of habitats in all climatic zones, including extremely stressful environments (Galloway 2008; Kappen 2000; Spribille 2018). On the other hand, lichens represent poikilohydric organisms that cannot actively regulate water content inside the body (Green et al. 2011). This feature makes thallus hydration closely dependent on the water availability from the environment. Lichens include both desiccation-sensitive and desiccation-tolerant species (Kranner

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et al. 2008). They are often exposed to desiccation and rehydration cycles, whose regularity and amplitude largely result from the climatic conditions that prevail in the growth environment (Jonsson Čabrajić et al. 2010). Lichens cope with this problem under their natural habitat conditions and remain viable, albeit they are inactive under dry conditions. Thallus desiccation rate and survival ability in a dry state depends on the species morphology and its physiological properties (Jonsson Čabrajić et al. 2010; Phinney et al. 2018; Renhorn et al. 1997). Functional hydration traits may even be intraspecifically variable depending on the structural features of the individuals (Gauslaa et al. 2019). The distribution and presence of lichens in a given environment seems to be clearly related to their humidity requirements and desiccation tolerance (Green et al. 1991; Munzi et al. 2019; Phinney et al. 2019).

Symbiotic coexistence requires good functioning of both algal and fungal components, and, consequently, the condition of one partner ultimately depends on the vitality of the other. Maintaining the optimal photosynthesis efficiency ensures adequate production of ribitol, which provides the precursors for the fungus metabolism (Eisenreich et al. 2011; Lines et al. 1989; Osyczka et al. 2021). Analysis of chlorophyll fluorescence (OJIP curve) aimed at assessing the efficiency of photosystem II (PSII) functioning has been successfully used to recognize the effect of various stress factors on the vitality, also in the context of desiccation, water balance, and environmental climatic conditions (e.g., Atala et al. 2015; Bednaříková et al. 2020a; Gauslaa and Solhaug 1996; Jonsson Čabrajić et al. 2010; Pirintsos et al. 2011). Photosynthetic activity of the algal component strictly depends on hydration status of the thallus (Hovind et al. 2020) and performance of lichens in relations to various sources and amount of water in a habitat; their capacity to reactivate with thallus rehydration appears to be essential for surviving in volatile environments (Jonsson Čabrajić et al. 2010). Sensitive hygrophilous lichens are particularly susceptible to changes in water relations in their natural sites of occurrence (Bianchi et al. 2020).

Most epiphytic lichens demonstrate high specificity to a habitat type, i.e., deforested or forest area. Generalist lichens constitute a relatively small group; they are fairly indifferent to microclimatic conditions and can grow on trees standing in nonforested and forest habitats (Kubiak and Osyczka 2020; Osyczka and Kubiak 2020). In contrast, stenoecious lichens are restricted to a narrow range of habitats and environmental conditions. Deciduous primeval forests provide a unique habitat resulting from a complex spatial structure shaped over a long period of time (Fritz et al. 2008). Many sensitive hygrophilous species find shelter only in such a habitat, and some of them are considered as old-growth forest indicators or relicts of ancient deciduous forests (e.g., Johansson and Gustafsson 2001; Motiejūnaitė et al. 2004; Nordén et al. 2007). Even subtle differences in microclimate parameters between forest complexes representing the same forest community may contribute to the presence or absence of a given lichen indicator (Kubiak and Osyczka 2017). Therefore, all external factors and those internal attributes at the organism level are crucial for the persistence of sensitive lichens in the environment (Gauslaa et al. 2012, 2019; Hovind et al. 2020; Jonsson Čabrajić et al. 2010; Osyczka and Myśliwa-Kurdziel 2023). The recognition of the ecological tolerance limits and physiological response to prolonged desiccation stress of old-growth forest lichens as well as identification of factors that may affect lichen spatial distribution in the face of climate change seems to be an urgent matter in the light of the reports on dramatic losses in the diversity of epiphytic lichens in temperate deciduous forests over the last century (Hauck et al. 2013).

Although the desiccation stress has been widely studied and discussed in relation to different lichen species, we wanted to gain a broader insight into the problem. We intended to (i) evaluate potential links between ecological patterns of epiphytic lichens and their photosynthetic functional traits in relation to highly and non-habitat-specific species; (ii) specify the relationship between the close attachment of stenoecious epiphytic lichens to a forest habitat in the context of their sensitivity to desiccation and reactivation rate upon rehydration; and (iii) assess to what extent tolerance to stress related to prolonged desiccation and lack of hydration events is species specific, and how far it results from ecological specificity of unrelated species with similar habitat requirements. With reference to the above, we set the general hypothesis: As opposed to generalist lichens, the narrow ecological amplitude of old-growth forest lichens is closely related to group-specific low tolerance to long-term desiccation stress and slow photosynthesis reactivation upon rehydration.

MATERIALS AND METHODS

Target sets of species.—Two sets of lichen species, which are ecologically distinct in terms of humidity requirements and confinement to old forest complexes (Cieśliński 2003; Motiejūnaitė et al. 2004; Wirth 2010), were designated for the study: (i) stenoecious (old-growth forest) lichens—*Cetrelia cetrarioides, Lobaria pulmonaria*, and *Menegazzia terebrata*; (ii) generalist lichens—*Flavoparmelia*

caperata, Hypogymnia physodes, and *Parmelia sulcata* (SUPPLEMENTARY FIG. 1). The selected lichens form heteromerous, relatively large-sized and broad-lobed thalli with lobe parts of regular and uniform upper surface. Internal cephalodia with cyanobacteria were present in the medulla of the examined *Lobaria* thalli. Despite the differences in the range of ecological tolerance, all these lichens can be found together in the interior of the forest at one locality in the sampling collection area (Kościelniak 2013).

Sampling site.—Lichen specimens were collected in the Bieszczady Mountains (Eastern Carpathians, southeast of Poland). According to the updated Köppen-Geiger classification (Kottek et al. 2006), the climate of this area has been assigned to Dfb type (snow climate, fully humid, warm summer). The mean annual temperature is slightly above 10 C, the mean sum of annual precipitation ranges from 900 (in mountain valleys) to above 1200 (in the higher parts of the mountains) mm, and relative humidity (RH) is about 77–84% (Nowosad 1995). All the lichen material was collected from one forest stand limited to an area of approximately 1 ha (valley of the Halicz stream, Górny San forest district, forest section no. 27). Therefore, it can be assumed that the populations of these lichens developed under the same topoclimatic conditions. This region is covered mainly by a lower montane beech forest with Carpathian beechwood (*Dentario glandulosae-Fagetum*) as the dominant type of the forest community.

Sampling time and initial sample preparation.—Lichen samples were collected at the beginning of summer season 2021. The thalli were taken together with fragments of their host substrate. A period of at least 3 days without any precipitation preceded the sampling dates. The climatic parameters for the 2-month period before sampling are illustrated in SUPPLEMENTARY FIG. 2.

The lichen material was prepared the next day after thalli collection. Whole fragments of thalli were transferred to a closed room providing stable conditions with reduced air humidity (temperature: ~18 C, RH: ~40%, light intensity during the day no more than 90 µmol photons m^{-2} s^{-1}, which corresponds to daylight in forest interior). The samples for analyses were cleaned and freed from macroscopic foreign materials adhering to the thallus surfaces. Well-developed, regular-shaped, and without excessive vegetative structures outer parts of the thalli were assigned for measurements (see Tretiach et al. 2005). Four rounds of examination related to desiccation stress and photosynthesis reactivation upon thallus rehydration were completed: (i) fresh samples collected at the beginning of summer (treated as reference) and samples exposed to (ii) 1-, (iii) 2-, and (iv) 3-month desiccation stress.

Relative water content and related photosynthetic activity of PSII.—The relative water content (RWC) in subsequent time intervals upon thallus rehydration was evaluated using the equation %RWC = [(Fw − Dw)/(Ww − Dw)] × 100, where Fw is the weight during the measurement (actual fresh weight), Dw is the dry weight, and Ww is the weight of fully hydrated sample (see, e.g., Barták et al. 2021). Evaluation was based on ca. 50 mg dry weight of lichen samples; the weight of a sample obtained after 24 h of rehydration was considered the state of fully hydrated thallus. The samples were maintained in wet state between time intervals, and excess water was removed by a quick shaking of the thallus prior to the weighing.

Fully hydrated and with maximum photosynthetic efficiency lichen samples of each species were brought into a weight corresponding to RWC of ca. 25%, 50%, and 75%. The relevant sample weights for each species were calculated and applied. During the desiccation process, the samples were under stable conditions with reduced air humidity (temperature: ~18 C, RH: ~40%). Analysis of chlorophyll fluorescence was performed when samples reached the appropriate weight for a given RWC. That way, the dependence of the level of photosynthetic efficiency (expressed by F_V/F_M) on the hydration state of thalli was estimated.

Chlorophyll fluorescence analysis (OJIP curve).—Photosynthetic efficiency was determined based on chlorophyll a (Chl a) fluorescence. Ten structurally complete and large thallus fragments of each species were sprayed until wet with rainwater harvested from the sampling area (pH 7.2, conductivity 27 µS cm^{-1}, the initial thallus moisture content before rehydration did not exceed 8%, assessed using the impedance technique; see Coxson 1991). After less than 1 h, the samples were inserted into leaf clips with 4 mm aperture diameter. Measurements were performed at several fixed time intervals after complete thallus rehydration, i.e., 1, 6, 12, and 24 h. Between subsequent time intervals, leaf clips were lifted up at an obtuse angle and the thalli rested freely on their lower part. The opened and loosened clips were carefully inserted into a transparent chamber providing very high relative humidity (close to 100% and not less than 99.8%). In this way, it was possible for fluorescence data records to refer to the same part of thallus each time. The analysis was performed using an

advanced continuous excitation chlorophyll fluorimeter, Handy PEA+ (Hansatech Instruments, King's Lynn, Norfolk, UK). Prior to measurements, the samples were adapted to darkness for 15 min. The Chl a fluorescence transients were induced by ultrabright red light (650 nm) provided by an array of three high-intensity LEDs (light-emitting diodes). Data were recorded after a saturating light pulse (2400 μmol photons m^{-2} s^{-1}) of 1 s; the gain of the PEA was 1.0. The transient curves of fast fluorescence kinetic and sequence of steps called OJIP were plotted for samples rehydrated for 1 h. A routinely used physiological indicator of photosynthetic efficiency, F_V/F_M, representing the potential quantum yield of primary photochemistry (Maxwell and Johnson 2000), was mainly employed to express the overall vitality of the lichen samples. Additionally, the performance index PI_{ABS}, a global indicator that is calculated from three independent components of PSII reaction center functioning (see Paoli et al. 2010; Strasser et al. 2004), and selected parameters related to energy fluxes and quantum yields, i.e., F_0, F_M, ABS/RC, DI_0/RC, Ψ_0, and φE_0, were also under consideration (for parameter specifications, see SUPPLEMENTARY TABLE 1). These parameters may indicate negative changes in PSII functioning or dissipation of absorbed energy. Abnormal (greatly decreased or increased) values are often associated with disturbed hydration status or drought stress (e.g., Bednaříková et al. 2020a; Kalaji 2011; Kalaji et al. 2016; Strasser et al. 2000).

Data processing.—The normality distribution was checked using the Kolmogorov-Smirnov test, and Levene's test was used to verify the homogeneity of variances; if necessary, the Box-Cox transformation was implemented. Depending on the purpose of data processing, one-way or two-way analysis of variance (ANOVA) was applied. The Tukey HSD (honestly significant difference) post hoc test was also used. The Kruskal-Wallis test was involved if the requirements for parametric test were violated. Nested design ANOVA was applied to verify differences in the F_V/F_M value between categorical factors "rehydration time interval," "set of species," and "lichen species" (nested within "set of species") to generally assess to what extent the variation was due to particular factors. The effect sizes were calculated for 1- and 2-month desiccation stress separately.

The curves of variable fluorescence were calculated from Chl a fluorescence induction curves according to the formula $Vt = (F_t - F_0)/(F_M - F_0)$. Before that, data points for 10 repetitions were averaged (n = 10). The OJIP curves were plotted on a log-time axis.

The radar charts (Supplemental Material) show the rate of photosynthesis reactivation based on the ratios of the mean values obtained from a given measurement series to the mean reference values determined for individual species. This allowed for a general comparison of the value levels of parameters that were measured on different scales and determined for different species.

RESULTS

Potential quantum yield of PSII against relative water content in thalli.—The growth rate of RWC in thalli of particular lichen species during the rehydration process is shown in FIG. 1A. Both "rehydration time interval" and "lichen species" affected RWC, and there was also significant interaction between those variables; for details on the main effects and their interaction, see SUPPLEMENTARY TABLE 2. One hour was enough to rehydrate the thalli at the RWC levels of 50% to 70%. After the first hour, relatively the lowest RWC was achieved by *H. physodes* and *M. terebrata* (however, the thalli of these lichens were characterized by the highest water holding capacity; data not shown). The thalli of *C. cetrarioides* and *L. pulmonaria* reached the state close to the highest RWC the fastest (these lichens, in turn, had the lowest water holding capacity; data not shown).

The value of F_V/F_M was affected by "relative water content" and "lichen species," and significant interaction between variables was also revealed; for details on the main effects and their interaction, see SUPPLEMENTARY TABLE 3. Samples of all species at RWC of 75% and 50% remained photosynthetic efficiency at a relatively stable and very high level. A significant decrease in the F_V/F_M values was recorded when the thalli desiccated to RWC of 25%. Nevertheless, despite the noticeable decrease, photosynthetic efficiency (F_V/F_M) was still at a high level, close to or above the value 0.7 for each species (FIG. 1B).

Fluorescence kinetics: OJIP test.—The fluorescence transient curves plotted for samples of all examined lichens collected at the beginning of summer and rehydrated for 1 h revealed the characteristic sequence of OJIP steps typical of healthy lichens (FIG. 2A). The curves of the relative variable fluorescence for samples exposed to long-term desiccation were disrupted compared with the reference ones (FIG. 2B, C vs. FIG. 2A). The increase in the O–J phase (appearance of K-band, the changes of amplitude of relative variable fluorescence expressed by increased ΔV_{OJ}; FIG. 2D) and consequently the flattening in the J–I and I–P phases (the changes of amplitude expressed by reduced ΔV_{JI} and ΔV_{IP}; FIG. 2D) were particularly evident for stenoecious lichens, especially *C. cetrarioides* and *M. terebrata*. This is highlighted

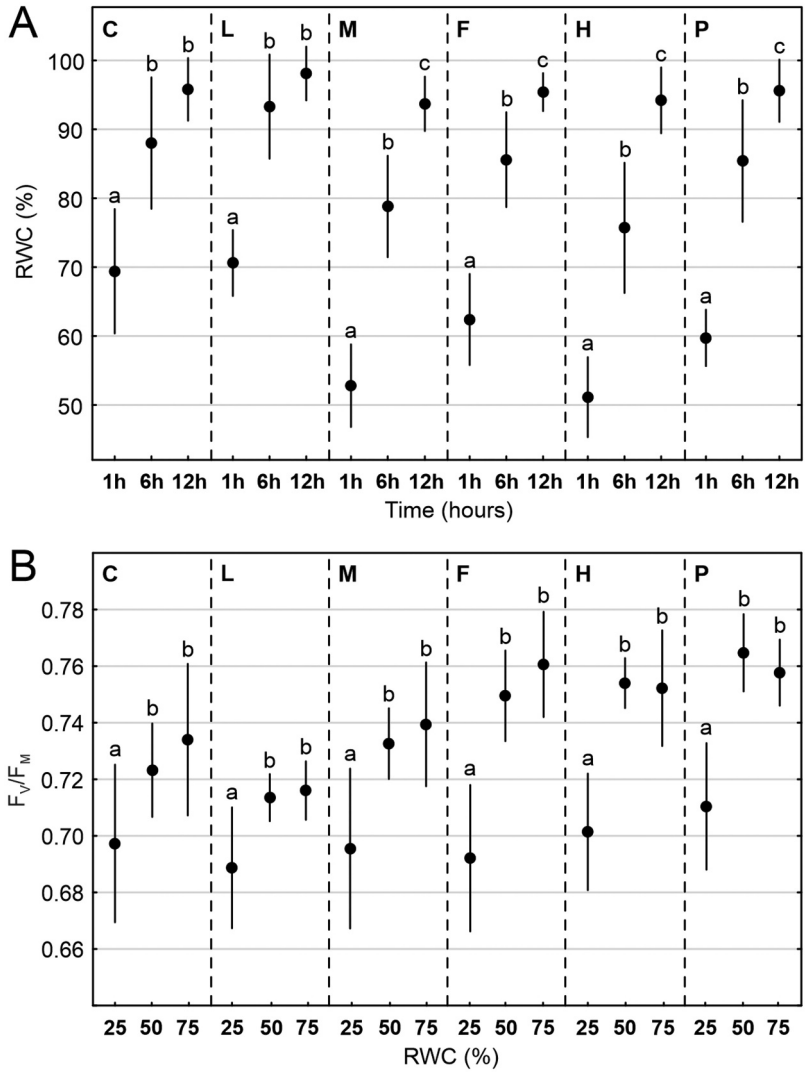

Figure 1. A. Changes in the relative water content (RWC; mean ± SD, n = 10) in thalli of particular lichen species upon rehydration. B. F_V/F_M values determined for thalli at a given RWC. The results of Tukey's (HSD) post hoc test performed for particular lichen species are provided; various letters indicate statistically significant differences ($P < 0.05$). For the result of two-way ANOVA and details on the main effects and interactions, see SUPPLEMENTARY TABLES 2 and 3. Lichen species: C = *Cetrelia cetrarioides*; L = *Lobaria pulmonaria*; M = *Menegazzia terebrata*; F = *Flavoparmelia caperata*; H = *Hypogymnia physodes*; P = *Parmelia sulcata*.

in the case of 2-month desiccation stress (FIG. 2C, D). Despite noticeable alternations, the curves of generalist lichens exposed to desiccation stress assumed sigmoid character after 1 h of rehydration (FIG. 2B, C).

Photosynthetic performance, chlorophyll fluorescence emission parameters.—The photosynthetic efficiencies measured in samples of all species collected at the beginning of summer were at a similar level, reaching a high value already 1 h after water supply. Although F_V/F_M for *C. cetrarioides* was the lowest compared with other lichens (with the exception of *L. pulmonaria*), the mean values fall within the range of 0.7–0.8 in all species (SUPPLEMENTARY FIG. 3A). The PI_{ABS} parameter turned out to be highly species dependent, and the value ranges were sometimes almost not overlapping between species (SUPPLEMENTARY FIG. 3B); for example, the mean values for *L. pulmonaria* and *P. sulcata* were roughly twice as high as for *C. cetrarioides*. The lowest values were recorded for *C. cetrarioides* and *H. physodes*, the highest for *L. pulmonaria* and *P. sulcata*, and the mean values for the other two species ranged from 0.4 to 0.6.

The nested ANOVA revealed that all factors included in the model significantly affected the F_V/F_M value. However, the output results showed that the effect size for "rehydration time interval" and "set of species" was much greater than that for "lichen species" (TABLE 1);

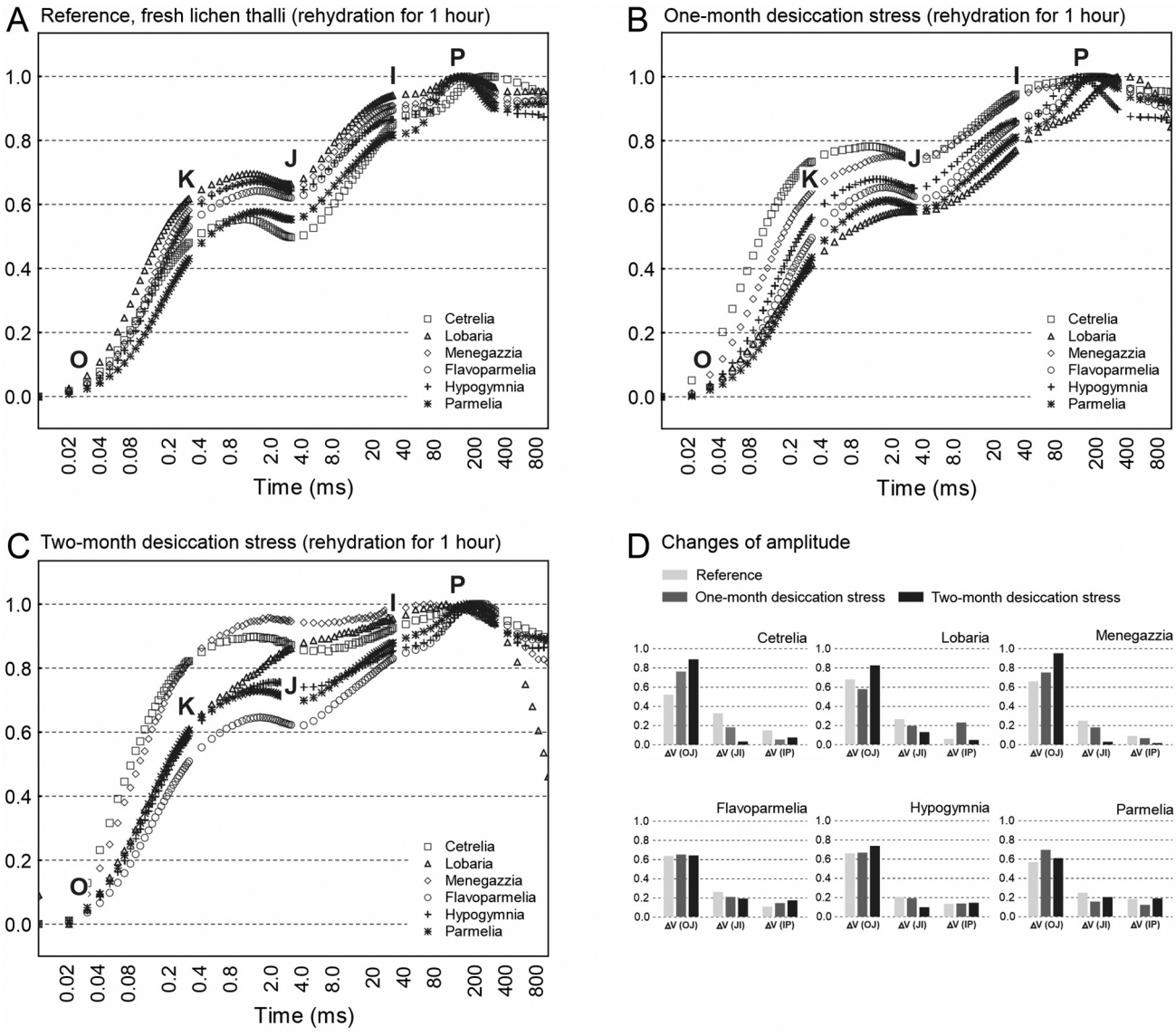

Figure 2. A–C. The curves of variable fluorescence calculated from chlorophyll a fluorescence induction curves (see Materials and Methods) for lichen thalli rehydrated for 1 h with respect to (A) reference (fresh lichen thalli), (B) 1-month, and (C) 2-month desiccation stress (the letters O, K, J, I, and P are positioned at the same place on each plot). The curves are plotted based on data points averaged for 10 repetitions. D. Changes in amplitude of relative variable fluorescence in O–J phase (ΔV_{OJ}), J–I phase (ΔV_{JI}), and I–P phase (ΔV_{IP}) for particular studied lichens.

Table 1. Results of nested ANOVA for the effect of "rehydration time interval" (TI), "set of species" (SS), and "lichen species" nested within SS (LS_{SS}) on the F_V/F_M value for 1- and 2-month desiccation stress.

Stress	Variable	Sum of squares	Mean square	*df*	η^2	*F*	*P*
One-month desiccation	TI	0.84	0.28	3	0.57	**103.09**	**<0.001**
	SS	0.44	0.44	1	0.41	**159.89**	**<0.001**
	LS_{SS}	0.08	0.02	4	0.11	**7.09**	**<0.001**
	Error	0.63	0.003	231			
Two-month desiccation	TI	3.79	1.26	3	0.67	**155.26**	**<0.001**
	SS	2.02	2.02	1	0.51	**248.86**	**<0.001**
	LS_{SS}	0.44	0.11	4	0.19	**13.50**	**<0.001**
	Error	1.87	0.008	231			

Note. Significant effects are provided in bold.

this concerned 1- and 2-month desiccation stress. The progression in PSII efficiency with successive time intervals clearly differed between the two sets of lichens (FIGS. 3 and 4); this is particularly pronounced in the case of 2-month desiccation period. Photobionts of stenoecious lichens responded to rehydration much slower in PSII activation (SUPPLEMENTARY FIG. 6). None of the samples approached the F_V/F_M level of 0.6 after 1 h, and the period of 6 h was usually insufficient to achieve this level (FIG. 3). Moreover, the activation for the thalli exposed to 2-month desiccation stress started with an average not exceeding the level of 0.2, and most of the *Cetrelia* and *Lobaria* samples did not reach the level of 0.6 even after 12 h of rehydration. Nevertheless, the F_V/F_M values for samples of all forest lichens were close to the reference or at least exceeded the value of 0.6 after 1 day of rehydration (FIG. 3). The photosynthesis activation in photobionts of generalist lichens proceeded much faster, and usually 1 h of rehydration was enough to achieve high efficiency (FIG. 3). The same applied to the PI_{ABS} parameter, although it should be noted that fluctuations in the parameter values within one species and a given measurement series were observed, especially in the case of *F. caperata* (FIG. 4). The initial values of PI_{ABS} for stenoecious lichens after 1 h of rehydration were always extremely low and slowly increased with the subsequent measurement series. Generalist lichens achieved the reference values much faster, at least if they were exposed only to 1-month desiccation stress (FIG. 4).

The photobionts of only generalist lichens, albeit with great irregularity, were able to activate PSII system after being desiccated for 3 months. Although the mean values of F_V/F_M increased in successive measurement series, greatly fluctuated records were obtained (SUPPLEMENTARY FIG. 7); this means, in fact, that not all samples were able to recover photosynthesis. No fluorescence signal was returned or the F_V/F_M values were far below 0.1 for all samples of forest lichens even after 24 h of rehydration.

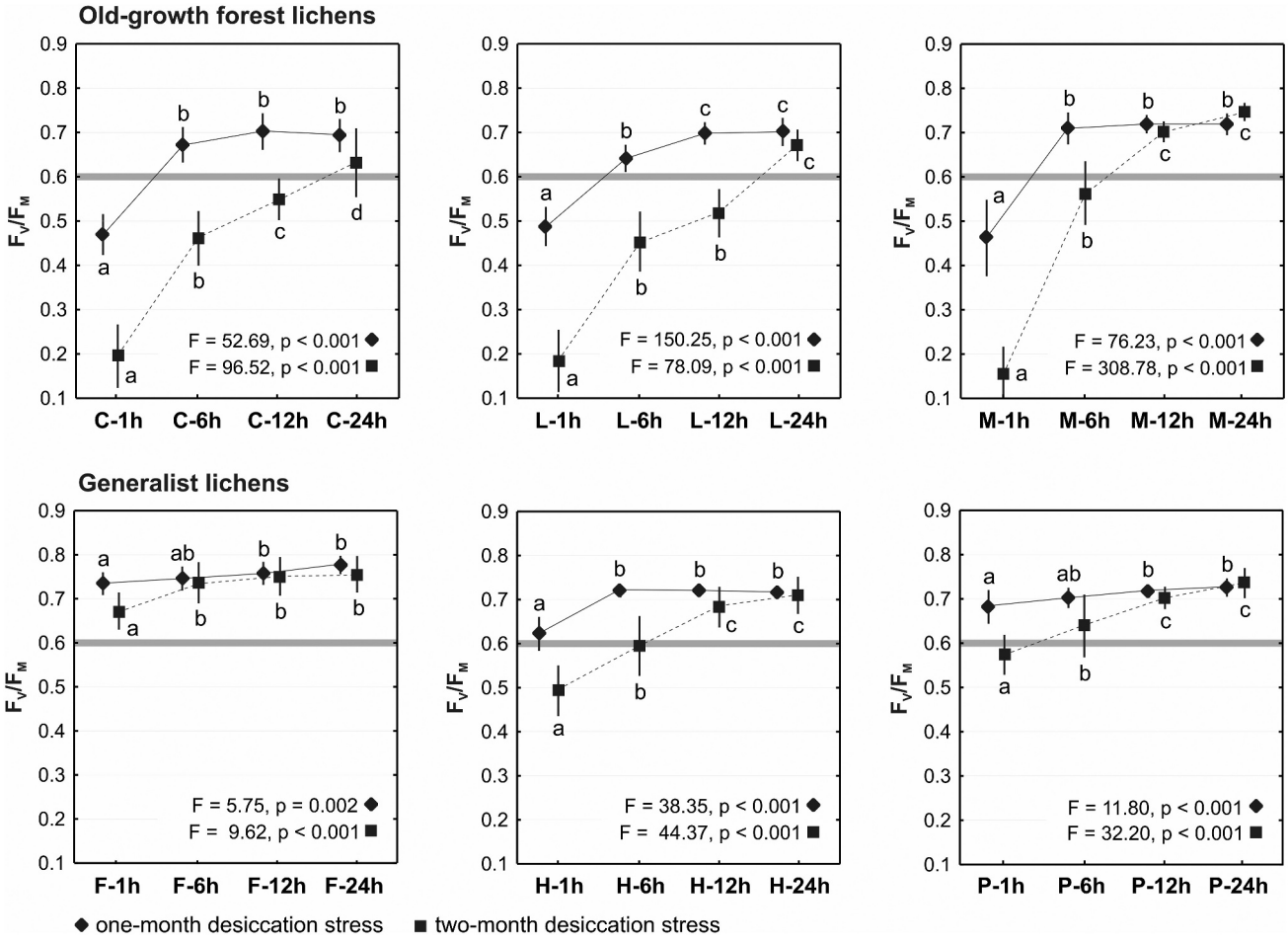

Figure 3. Changes in the F_V/F_M value (mean ± SD, n = 10) for thalli of particular lichen species in subsequent time intervals upon rehydration. The results of one-way ANOVA (*F* and *P* values) and Tukey's (HSD) post hoc test performed for particular desiccation stress are provided; various letters indicate statistically significant differences ($P < 0.05$). Gray line marks the level 0.6 corresponding to healthy chlorolichens. Lichen species as in FIG. 1.

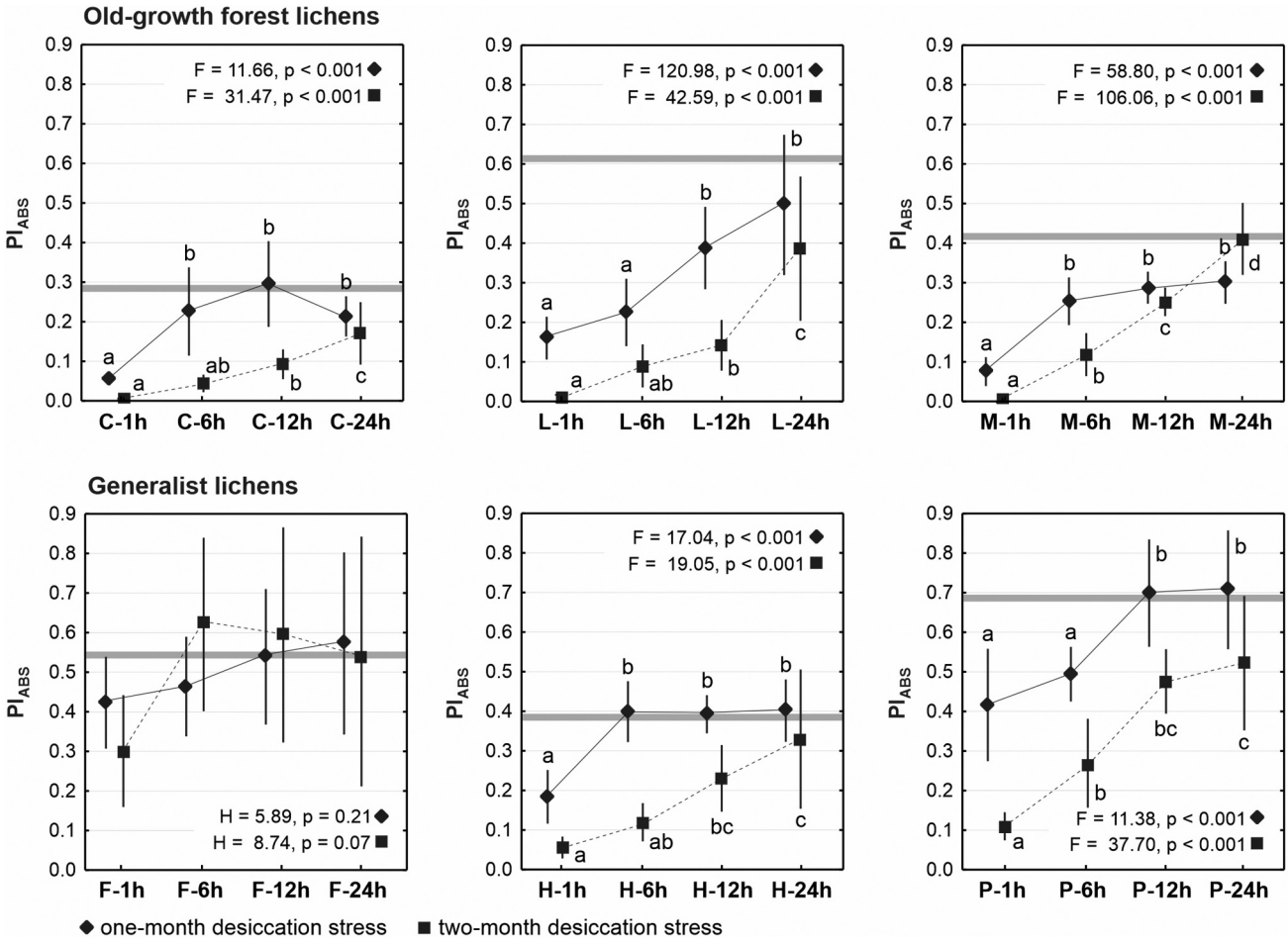

Figure 4. Changes in the performance index PI_{ABS} value (mean ± SD, n = 10) for thalli of particular lichen species in subsequent time intervals upon rehydration. The results of one-way ANOVA (*F* and *P* values) or the Kruskal-Wallis test (*H* and *P* values) and Tukey's (HSD) post hoc test performed for particular desiccation stress are provided; various letters indicate statistically significant differences ($P < 0.05$). Gray line marks the mean reference value determined for a given lichen species. Lichen species as in FIG. 1.

Differences between lichens in the PSII functionality, expressed by gradual changes in the values of selected parameters measured in successive time intervals upon thallus rehydration, are visualized on the radar charts (SUPPLEMENTARY FIGS. 4 and 5). Extremely elevated values of parameters related to energy fluxes through PSII, i.e., ABS/RC and DI_0/RC, and decreased values of parameters related to electron transport, i.e., Ψ_0 and φE_0, were recorded in forest lichens. This is especially noticeable for the first time intervals and in the case of 2-month desiccation stress. Strong deviations from the reference values apply to a much greater extent to forest lichens than to generalist lichens. Moreover, in the first rehydration time intervals, disadvantageous relation of the value F_0 to F_M (high F_0 and low F_M) was usually more pronounced in old-growth forest lichens. Anomalous parameter values clearly progressed faster toward the reference levels along with the rehydration time in the samples of generalist lichens. The most regular polygons and the closest to the reference were usually obtained for *F. caperata*.

DISCUSSION

The hygrophilous species *C. cetrarioides, L. pulmonaria*, and *M. terebrata* are frequently used as old-growth forest and/or forest ecological continuity indicators (Coppins and Coppins 2002; Motiejūnaitė et al. 2004). Strong affinity to a forest habitat results directly from a suitable microclimate provided by the forest and also indirectly from a complexity of factors nested within regional bioclimatic gradients (Nordén et al. 2014). Even small disturbances in natural sites of stenoecious lichens may have a limiting effect on them (Bianchi et al. 2020; Nascimbene et al. 2016). Evidence has been provided that the occurrence of *L. pulmonaria* is controlled by a delicate balance between light availability and desiccation risk. Physiological trade-off between the

growth potential and irreversible damage resulting from desiccation, paradoxically both of which increase with increasing light, limits the species to old forests (Gauslaa et al. 2006). In contrast, although three other studied species (*F. caperata, H. physodes, P. sulcata*) are widespread across woodlands, the specific microclimate of an old forest interior is not a precursor to their presence; basically, they prefer rather exposed sites (Nimis 2022).

Lichen growth and their potential to spread depend on the photosynthesis rate performed by photobionts, and this is strictly dependent on the status of lichen thallus hydration (Gasulla et al. 2021; Green et al. 2008; Kranner et al. 2003). It is believed that lichens are metabolically active when their water content exceeds 40% of the dry weight (Sundberg et al. 1996). For lichens that do not have special internal water regulation mechanisms, short-term climatic fluctuations and long-term changes in the environment are of great importance for their functioning, whereby the latter may determine the persistence of a given species. Liquid water, in the form of rain, dew, or surface flow, hydrates thalli almost immediately. Hydration with high air humidity is much slower and less efficient (Hovind et al. 2020; Jonsson et al. 2008; Lange et al. 1986; Rundel 1988). Nevertheless, humid air is still very important, basically salutary, for lichens, since it prolongs the hydration period induced by rain and improves the chances of recovery, especially in species with a slow activation rate (Jonsson Čabrajić et al. 2010). Although the decline in the F_V/F_M value for lichen thalli with RWC of 25% was noticed, PSII activity remained at a relatively very high level for each studied species. Similarly, Barták et al. (2021) observed species-specific fall in F_V/F_M starting at an RWC range of 22–32%, whereas the involvement of protective mechanisms in the chloroplastic apparatus of lichen photobionts was noticed only at RWC of below 20%. Negative changes in PSII functioning at very low RWC (e.g., decrease in φE_0 parameter) are associated with limitations of the photosynthetic linear electron flow (Bednaříková et al. 2020a). The length of time with hydration at a satisfactory level rather than very high level of RWC is of the greatest importance for old-growth forest lichens.

The length of time a species can survive in the desiccated state and the recovery rate determinate the possibility of appearance and survival of this species in a given habitat type. The abilities in this regard are sometimes surprising; some sturdy lichens can be revivified after being desiccated under laboratory conditions for several months. Nevertheless, metabolic inactivation for such a long period and prolonged desiccation lead to gradual dying of thalli (Kranner et al. 2008). For example, the lichens *Lobaria pulmonaria, Peltigera polydactyla*, and *Pseudevernia furfuracea* can survive desiccated at thallus water contents less than 6% for 2 months, although during long-term desiccation the photobionts of the first two species gradually lose viability (Kranner 2002; Kranner et al. 2003). Desiccation is not only a problem related to the inability to conduct proper metabolic processes, such as photosynthesis or respiration. The lack of water causes loss of cellular integrity and eventually leads to cellular collapse (Gasulla et al. 2021; Kranner et al. 2008). Similarly to generalists, healthy hygrophilous lichens that thrive in their natural habitat with stable microclimatic conditions do not require long time to regain a high level of photosynthesis efficiency upon direct rehydration after a short rainless period (Osyczka 2022). Nevertheless, lichens with slow hydration and low equilibrium water content are at risk of remaining inactive or with reduced photosynthetic efficiency, even under impeccable humidity conditions (Hovind et al. 2020; Jonsson Čabrajić et al. 2010). The fluorescence transient curves for old-growth forest lichens upon 1 h of rehydration differ far more from the reference ones than in the case of generalist lichens. This is especially noticeable for 2-month desiccation stress. The clear K-band and, consequently, increased ΔV_{OJ} may be related to the impairment of oxygen-evolving complex and inhibition of donating electrons to PSII due to heat or drought and high-light stresses (Strasser et al. 2004). The suppressed I–P phase and simultaneously very low value of ΔV_{IP} may indicate some slowed electron transport by downstream electron carriers associated with the oxidation and reduction of PSI (see also Osyczka and Myśliwa-Kurdziel 2023). The deactivation of the photosynthesis process and the absence or weak Chl a fluorescence may also be related to a long-wavelength quencher embedded in the antenna complex that protects PSII from photodamage. Experimental evidence has been provided that such a mechanism occurs in trebouxioid photobionts (Heber 2008; Komura et al. 2010; Verrman et al. 2007), and the quencher would capture the absorbed energy faster than the reaction centers, dissipating it as heat. The quenching process progresses with the drying of thalli, and the rate of quencher activation depends on the drying rate of the algal cells (Gasulla et al. 2009). In parallel, some time is needed to progressively extinguish this protective mechanism in the following rehydration cycle. The inability to instant deactivate the quencher by the fast rehydration process may result in low F_V/F_M values (Tretiach et al. 2012). Increased values of ABS/RC and DI_0/RC reflect increase in dissipation of absorbed energy by nonphotochemical processes (Marečková et al. 2019). Barták et al. (2018) proved that ABS/RC increased with dehydration of algal

photobiont in *Dermatocarpon polyphyllizum*. Similarly, Barták et al. (2015) suggested that the number of active reaction centers of PSII in the Arctic lichens of genus *Umbilicaria* was likely to be reduced by dehydration. Thermal dissipation, expressed by increased DI_0/RC, represents another sensitive parameter pointing to the involvement of PSII protective mechanisms activated during desiccation stress in lichen photobionts (Bednaříková et al. 2020b). A reduced value of Ψ_0 parameter indicates that the use of energy to power the electron transport is not yet optimal. Since the energy absorbed by the antennas is dissipated (increased value of DI_0/RC), it is used to a lesser extent to activate the electron transport (decreased value of Ψ_0 and φE_0) (Bednaříková et al. 2020b).

Regardless of the peculiarities of deactivating the photosynthesis process, the growing season for many lichens may be much shorter than their summarized wet period. In addition, the frequency and length of hydration events also affects the performance in a habitat of lichens with slow photosynthetic activation rates. Brief and intermittent periods of wet time may hamper realized activity severely (Jonsson Čabrajić et al. 2010). For example, slow activation kinetics significantly reduced realized activities for *Platismatia norvegica*, and even more dramatically for *Bryoria bicolor* and *Usnea longissima* (Jonsson Čabrajić et al. 2010). The prolonged period of desiccation and metabolic inactivation may pose a critical problem for old-growth forest lichens. Moreover, experimental evidence has been provided that functional plasticity of the photosynthetic apparatus of photobionts largely determines the dispersal abilities of lichens (Osyczka and Myśliwa-Kurdziel 2023). All three species examined in this study exhibit considerably more sluggish PSII activation upon rehydration compared with all three generalist lichens. For forest lichens, an hour of direct contact with water is not enough to induce photosynthesis at fairly normal level after a month of desiccation and about half a day of full hydration is needed to approach the F_V/F_M level near the value 0.6 when desiccation lasted for 2 months. In contrast, generalist lichens are able to activate PSII system quite promptly, even after being dry for 2 months. The phenomenon, therefore, can be considered broadly in the context of the entire ecological group of lichens and not only as the specificity of individual species (see also TABLE 1). This probably implies difference between spatial distribution of forest and generalist lichens, especially when taking into account the realities of the natural environment and field performance of lichens (see Jonsson Čabrajić et al. 2010; Lange et al. 2001; Pintado et al. 1997; Pirintsos et al. 2011).

Conclusions.—Lichens of two distinct ecological sets, i.e., old-growth forest (*C. cetrarioides, L. pulmonaria, M. terebrata*) and generalist (*F. caperata, H. physodes, P. sulcata*) differ considerably in terms of sensitivity to desiccation stress. Moreover, delayed and fast activation of the photosynthesis process upon rehydration characterize the sets, respectively. The differences between the species within the sets are not so apparent. Contrary to generalist lichens, retrieving of photosynthesis after 3-month desiccation failed in old-growth forest lichens. In the long term, climate change and resulting prolonged rainless periods and an unfavorable water balance in the environment that are expected in the future may have a negative impact on realized activity of old-growth forest lichens during growing season. The tolerance range of lichens to desiccation stress results largely from the properties related to the activation of photosynthesis process after a prolonged period of water deficit.

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LITERATURE CITED

Atala C, Schneider C, Bravo G, Quilodrán M, Vargas R. 2015. Anatomical, physiological and chemical differences between populations of *Pseudocyphellaria flavicans* (Hook. f. & Taylor) Vain. from Chile. Gayana Bot. 72:21–26. doi:10.4067/S0717-66432015000100003.

Barták M, Hájek J, Orekhova A, Villagra J, Marín C, Palfner G, Casanova-Katny A. 2021. Inhibition of primary photosynthesis in desiccating Antarctic lichens differing in their photobionts, thallus morphology, and spectral properties.

Microorganisms. 9:818. doi:10.3390/microorganisms9040818.
Barták M, Mishra KB, Marečková M. 2018. Spectral reflectance indices sense desiccation induced changes in the thalli of Antarctic lichen *Dermatocarpon polyphyllizum*. Czech Polar Rep. 8:249–59. doi:10.5817/CPR2018-2-21.
Barták M, Trnková K, Hansen ES, Hazdrová J, Skácelová K, Hájek J, Forbelská M. 2015. Effect of dehydration on spectral reflectance and photosynthetic efficiency in *Umbilicaria arctica* and *U. hyperborea*. Biol Plant. 59:357–65. doi:10.1007/s10535-015-0506-1.
Bednaříková M, Folgar-Cameán Y, Kučerová Z, Lazár D, Špundová M, Hájek J, Barták M. 2020b. Analysis of K- and L-band appearance in OJIPs in Antarctic lichens in low and high temperature. Photosynthetica. 58:646–56. doi:10.32615/ps.2019.180.
Bednaříková M, Váczi P, Lazár D, Barták M. 2020a. Photosynthetic performance of Antarctic lichen *Dermatocarpon polyphyllizum* when affected by desiccation and low temperatures. Photosynth Res. 145:159–77. doi:10.1007/s11120-020-00773-4.
Bianchi E, Benesperi R, Brunialti G, Di Nuzzo L, Fačkovcová Z, Frati L, Giordani P, Nascimbene J, Ravera S, Vallese C, et al. 2020. Vitality and growth of the threatened lichen *Lobaria pulmonaria* (L.) Hoffm. in response to logging and implications for its conservation in Mediterranean Oak Forests. Forests. 11:995. doi:10.3390/f11090995.
Cieśliński S. 2003. Atlas rozmieszczenia porostów (Lichenes) w Polsce Północno-Wschodniej. Phytocoenosis 15 (NS). Suppl Cartograph Geobot. 15:1–426.
Coppins AM, Coppins BJ. 2002. Indices of ecological continuity for Woodland Epiphytic lichen habitats in the British Isles. London (UK): British Lichen Society.
Coxson D. 1991. Impedance measurement of thallus moisture content in lichens. Lichenologist. 23:77–84. doi:10.1017/S0024282991000130.
Eisenreich W, Knispel N, Beck A. 2011. Advanced methods for the study of the chemistry and the metabolism of lichens. Phytochem Rev. 10:445–56. doi:10.1007/s11101-011-9215-3.
Fritz Ö, Gustafsson L, Larsson K. 2008. Does forest continuity matter in conservation? – a study of epiphytic lichens and bryophytes in beech forests of Southern Sweden. Biol Conserv. 141:655–68. doi:10.1016/j.biocon.2007.12.006.
Galloway DJ. 2008. Lichen biogeography. In: Nash TH III, editor. Lichen biology. 2nd ed. Cambridge (NY): Cambridge University Press. p. 315–35.
Gasulla F, Del Campo EM, Casano LM, Guéra A. 2021. Advances in understanding of desiccation tolerance of lichens and lichen-forming algae. Plants. 10:807. doi:10.3390/plants10040807.
Gasulla F, de Nova PG, Esteban-Carrasco A, Zapata JM, Barreno E, Guéra A. 2009. Dehydration rate and time of desiccation affect recovery of the lichenic algae *Trebouxia erici*: alternative and classical protective mechanisms. Planta. 231:195–208. doi:10.1007/s00425-009-1019-y.
Gauslaa Y, Coxson D, Solhaug KA. 2012. The paradox of higher light tolerance during desiccation in rare old forest cyanolichens than in more widespread co-occurring chloro- and cephalolichens. New Phytol. 195:812–22. doi:10.1111/j.1469-8137.2012.04221.x.
Gauslaa Y, Johlander S, Nordén B. 2019. *Lobaria amplissima* thalli with external cephalodia need more rain than thalli without. Lichenologist. 51:281–86. doi:10.1017/S0024282919000197.
Gauslaa Y, Lie M, Solhaug KA, Ohlson M. 2006. Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. Oecologia. 147:406–16. doi:10.1007/s00442-005-0283-1.
Gauslaa Y, Solhaug KA. 1996. Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. Funct Ecol. 10:344–54. doi:10.2307/2390282.
Green TGA, Kilian E, Lange OL. 1991. *Pseudocyphellaria dissimilis*. a desiccation-sensitive, highly shade-adapted lichen from New Zealand. Oecologia. 85:498–503. doi:10.1007/BF00323761.
Green TGA, Nash TH III, Lange OL. 2008. Physiological ecology of carbon dioxide exchange. In: Nash TH III, editor. Lichen biology. 2nd ed. Cambridge (NY): Cambridge University Press. p. 152–81.
Green TGA, Sancho LG, Pintado A. 2011. Ecophysiology of desiccation/rehydration cycles in mosses and lichens. Ecol Stud. 215:89–120.
Hauck M, de Bruyn U, Leuschner C. 2013. Dramatic diversity losses in epiphytic lichens in temperate broad-leaved forests during the last 150 years. Biol Conserv. 157:136–45. doi:10.1016/j.biocon.2012.06.015.
Heber U. 2008. Photoprotection of green plants: a mechanism of ultra-fast thermal energy dissipation in desiccated lichens. Planta. 228:641–50. doi:10.1007/s00425-008-0766-5.
Hovind ABÅ, Phinney NH, Gauslaa Y. 2020. Functional trade-off of hydration strategies in old forest epiphytic cephalolichens. Fungal Biol. 124:903–13. doi:10.1016/j.funbio.2020.07.008.
Johansson P, Gustafsson L. 2001. Red-listed and indicator lichens in woodland key habitats and production forests in Sweden. Can J For Res. 31:1617–28. doi:10.1139/x01-091.
Jonsson Čabrajić AV, Lidén M, Lundmark T, Ottosson-Löfvenius M, Palmqvist K. 2010. Modelling hydration and photosystem II activation in relation to in situ rain and humidity patterns: a tool to compare performance of rare and generalist epiphytic lichens. Plant Cell Environ. 33:840–50. doi:10.1111/j.1365-3040.2009.02110.x.
Jonsson AV, Moen J, Palmqvist K. 2008. Predicting lichen hydration using biophysical models. Oecologia. 156:259–73. doi:10.1007/s00442-008-0990-5.
Kalaji HM. 2011. Oddziaływanie abiotycznych czynników stresowych na fluorescencję chlorofilu w roślinach wybranych odmian jęczmienia *Hordeum vulgare* L. Rozprawy Naukowe i Monografie (Treatises and Monographs). Warszawa (PL): Wydawnictwo SGGW.
Kalaji HM, Jajoo A, Oukarroum A, Brestic M, Zivcak M, Samborska IA, Cetner MD, Łukasik I, Goltsev V, Ladle RJ. 2016. Chlorophyll a fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions. Acta Physiol Plant. 38:102. doi:10.1007/s11738-016-2113-y.
Kappen L. 2000. Some aspects of the great success of lichens in Antarctica. Antarct Sci. 12:314–24. doi:10.1017/S0954102000000377.

Komura M, Yamagishi A, Shibata Y, Iwasaki I, Itoh S. 2010. Mechanism of strong quenching of photosystem II chlorophyll fluorescence under drought stress in a lichen, Physciella melanchla, studied by subpicosecond fluorescence spectroscopy. Biochim Biophys Acta - Bioenerg. 1797:331–38. doi:10.1016/j.bbabio.2009.11.007.

Kościelniak R. 2013. Lichens of the Bieszczady National Park – present state and changes in the last 50 years. Ustrzyki Dolne, Kraków (PL): Monografie Bieszczadzkie 14.

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World Map of the Köppen-Geiger climate classification updated. Meteorol Zeitschrift. 15:259–63. doi:10.1127/0941-2948/2006/0130.

Kranner I. 2002. Glutathione status correlates with different degrees of desiccation tolerance in three lichens. New Phytol. 154:451–60. doi:10.1046/j.1469-8137.2002.00376.x.

Kranner I, Beckett RP, Hochman A, Nash TH III. 2008. Desiccation-tolerance in lichens: a review. Bryologist. 111:576e593. doi:10.1639/0007-2745-111.4.576.

Kranner I, Zorn M, Turk B, Wornik S, Beckett RP, Batič F. 2003. Biochemical traits of lichens differing in relative desiccation tolerance. New Phytol. 160:167–76. doi:10.1046/j.1469-8137.2003.00852.x.

Kubiak D, Osyczka P. 2017. Specific vicariance of two primeval lowland forest lichen indicators. Environ Manage. 59:966–81. doi:10.1007/s00267-017-0833-4.

Kubiak D, Osyczka P. 2020. Non-forested vs forest environments: the effect of habitat conditions on host tree parameters and the occurrence of associated epiphytic lichens. Fungal Ecol. 47:100957. doi:10.1016/j.funeco.2020.100957.

Lange OL, Green TG, Heber U. 2001. Hydration-dependent photosynthetic production of lichens: what do laboratory studies tell us about field performance? J Exp Bot. 52:2033–42. doi:10.1093/jexbot/52.363.2033.

Lange OL, Kilian E, Ziegler H. 1986. Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. Oecologia. 71:104–10. doi:10.1007/BF00377327.

Lines CEM, Ratcliffe RG, Rees TAV, Southon TE. 1989. A 13C NMR study of photosynthate transport and metabolism in the lichen *Xanthoria calcicola* Oxner. New Phytol. 111:447–56. doi:10.1111/j.1469-8137.1989.tb00707.x.

Marečková M, Barták M, Hájek J. 2019. Temperature effects on photosynthetic performance of Antarctic lichen *Dermatocarpon polyphyllizum*: a chlorophyll fluorescence study. Polar Biol. 42:685–701. doi:10.1007/s00300-019-02464-w.

Maxwell K, Johnson GN. 2000. Chlorophyll fluorescence – a practical guide. J Exp Bot. 51:659–68. doi:10.1093/jexbot/51.345.659.

Motiejūnaitė J, Czyżewska K, Cieśliński S. 2004. Lichens – indicators of old-growth forests in biocentres of Lithuania and North-East Poland. Bot Lith. 10:59–74.

Munzi S, Varela Z, Paoli L. 2019. Is the length of the drying period critical for photosynthesis reactivation in lichen and moss components of biological soil crusts? J Arid Environ. 166:86–90. doi:10.1016/j.jaridenv.2019.04.019.

Nascimbene J, Casazza G, Benesperi R, Catalano I, Cataldo D, Grillo M, Isocrono D, Matteucci E, Ongaro S, Potenza G, et al. 2016. Climate change fosters the decline of epiphytic *Lobaria* species in Italy. Biol Conserv. 201:377–84. doi:10.1016/j.biocon.2016.08.003.

Nimis PL. 2022. ITALIC - the information system on Italian lichens. Version 7.0. University of Trieste, Department of Biology. https://dryades.units.it/italic.

Nordén B, Dahlberg A, Brandrud TE, Fritz Ö, Ejrnaes R, Ovaskainen O. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. Ecoscience. 21:34–45. doi:10.2980/21-1-3667.

Nordén B, Paltto H, Götmark F, Wallin K. 2007. Indicators of biodiversity, what do they indicate? Lessons for conservation of cryptogams in oak-rich forest. Biol Conserv. 135:369–79. doi:10.1016/j.biocon.2006.10.007.

Nowosad M. 1995. Zarys klimatu bieszczadzkiego parku narodowego i jego otuliny w świetle dotychczasowych badań. Roczniki Bieszczadzkie. 4:163–83.

Osyczka P. 2022. Hygrophilous old-growth forest lichens are highly capable of instantaneous photosynthesis activation after short-term desiccation stress. Acta Biol Crac Ser Bot. 64(1):15–25. doi:10.24425/abcsb.2022.142048.

Osyczka P, Kubiak D. 2020. Data on epiphytic lichens and their host-trees in relation to non-forested area and natural deciduous lowland forest. Data Br. 31:105711. doi:10.1016/j.dib.2020.105711.

Osyczka P, Latkowska E, Rola K. 2021. Metabolic processes involved with sugar alcohol and secondary metabolite production in the hyperaccumulator lichen *Diploschistes muscorum* reveal its complex adaptation strategy against heavy-metal stress. Fungal Biol. 125:999–1008. doi:10.1016/j.funbio.2021.08.002.

Osyczka P, Myśliwa-Kurdziel B. 2023. The pattern of photosynthetic response and adaptation to changing light conditions in lichens is linked to their ecological range. Photosynth Res. 157(1):21–35. doi:10.1007/s11120-023-01015-z.

Paoli L, Pirintsos SA, Kotzabasis K, Pisani T, Navakoudis E, Loppi S. 2010. Effects of ammonia from livestock farming on lichen photosynthesis. Environ Pollut. 158:2258–65. doi:10.1016/j.envpol.2010.02.008.

Phinney NH, Solhaug KA, Gauslaa Y. 2018. Rapid resurrection of chlorolichens in humid air: specifc thallus mass drives rehydration and reactivation kinetics. Environ Exp Bot. 148:184–91. doi:10.1016/j.envexpbot.2018.01.009.

Phinney NH, Solhaug KA, Gauslaa Y. 2019. Photobiont-dependent humidity threshold for chlorolichen photosystem II activation. Planta. 250:2023–31. doi:10.1007/s00425-019-03282-4.

Pintado A, Valladares F, Sancho LG. 1997. Exploring phenotypic plasticity in the Lichen *Ramalina capitata*: morphology, water relations and chlorophyll content in North- and South-facing populations. Ann Bot. 80:345–53. doi:10.1006/anbo.1997.0453.

Pirintsos SA, Paoli L, Loppi S, Kotzabasis K. 2011. Photosynthetic performance of lichen transplants as early indicator of climatic stress along an altitudinal gradient in the arid Mediterranean area. Clim Change. 107:305–28. doi:10.1007/s10584-010-9989-0.

Renhorn K-E, Esseen P-A, Palmqvist K, Sundberg B. 1997. Growth and vitality of epiphytic lichens. Oecologia. 109:1–9. doi:10.1007/s004420050051.

Rundel PW. 1988. Water relations, and Galun M, editor. Handbook of lichenology. Vol. 2. Boca Raton (FL): CRC Press; p. 17–36.

Spribille T. 2018. Relative symbiont input and the lichen symbiotic outcome. Curr Opin Plant Biol. 44:57–63. doi:10.1016/j.pbi.2018.02.007.

Strasser RJ, Srivastava A, Tsimilli-Michael M. 2000. The fluorescence transient as a tool to characterise and screen photosynthetic samples. In: Yunus M, Pathre U, Mohanty P, editors. Probing photosynthesis: mechanisms, regulation and adaptation. London (UK): Taylor & Francis; p. 445–83.

Strasser RJ, Tsimilli-Michael M, Srivastava A. 2004. Analysis of the chlorophyll a fluorescence transient. In: Papageorgiou GC, Govindjee G, editors. Chlorophyll a fluorescence. advances in photosynthesis and respiration. Vol. 19. Dordrecht (NL): Springer; p. 321–62.

Sundberg B, Palmqvist K, Esseen P-A, Renhorn K-E. 1996. Growth and vitality of epiphytic lichens. II. Modelling of carbon gain using field and laboratory data. Oecologia. 109:10–18. doi:10.1007/s004420050052.

Tretiach M, Baruffo L, Piccotto M. 2012. Effects of Mediterranean summer conditions on chlorophyll a fluorescence emission in the epiphytic lichen *Flavoparmelia soredians*: a field study. Plant Biosyst. 146:171–80. doi:10.1080/11263504.2012.727881.

Tretiach M, Crisafulli P, Pittao E, Rinino S, Roccotiello E, Modenesi P. 2005. Isidia ontogeny and its effect on the CO_2 gas exchanges of the epiphytic lichen *Pseudevernia furfuracea* (L.) Zopf. Lichenologist. 37:445–62. doi:10.1017/S0024282905014982.

Verrman J, Vasil'ev S, Paton GD, Ramanauskas J, Bruce D. 2007. Photoprotection in the lichen *Parmelia sulcata*: the origins of desiccation-induced fluorescence quenching. Plant Physiol. 145:997–1005. doi:10.1104/pp.107.106872.

Wirth V. 2010. Okologische Zeigerwerte von Flechten – erweiterte und aktualisierte Fassung. Herzogia. 23:229–48. doi:10.13158/heia.23.2.2010.229.